

Biogeochemical legacy of prescribed fire in a giant sequoia–mixed conifer forest: A 16-year record of watershed balances

Diana L. Engle,¹ James O. Sickman,² Claudette M. Moore,³ Annie M. Esperanza,⁴ John M. Melack,⁵ and Jon E. Keeley^{6,7}

Received 11 December 2006; revised 16 August 2007; accepted 25 September 2007; published 16 February 2008.

[1] The effects of prescription burning on watershed balances of major ions in mixed conifer forest were examined in a 16-year paired catchment study in Sequoia National Park, California. The objective was to determine whether fire-related changes in watershed balances persist as long as estimated low-end natural fire-return intervals (≤ 10 years), and whether cumulative net export caused by fire could deplete nutrient stocks between successive fires. Inputs (wet + dry deposition) and outputs (stream export) of N, S, Cl^- , HCO_3^- , Ca^{2+} , Mg^{2+} , Na^+ , K^+ , H^+ , and SiO_2 were measured for 7 years preceding, and 9 years following, a prescribed burn of one of the catchments. After fire, runoff coefficients increased by 7% (in dry years) to 35% (in wet years). Inorganic N was elevated in stream water for 3 years after fire. Increased export of water, SO_4^{2-} , Cl^- , SiO_2 , and base cations continued through the end of the study. Pools and processes attributed to fire led to the cumulative loss, per hectare, of 1.2 kg N, 16 kg S, 25 kg Cl^- , 130 kg Ca^{2+} , 19 kg Mg^{2+} , 71 kg Na^+ , 29 kg K^+ and 192 kg Si, above that predicted by prefire regression equations relating export in the paired catchments. This additional export equaled $<1\%$ of the N, up to one-third of the Ca and Mg, and up to three-fourths of the K, contained in the forest floor prior to combustion. Changes in watershed balances indicated that low-end natural fire-return intervals may prevent complete reaccumulation of several elements between fires.

Citation: Engle, D. L., J. O. Sickman, C. M. Moore, A. M. Esperanza, J. M. Melack, and J. E. Keeley (2008), Biogeochemical legacy of prescribed fire in a giant sequoia–mixed conifer forest: A 16-year record of watershed balances, *J. Geophys. Res.*, 113, G01014, doi:10.1029/2006JG000391.

1. Introduction

[2] Watershed balances in forests are affected by fire on a variety of timescales. Immediate losses of elements occur through volatilization [Caldwell *et al.*, 2002; Johnson *et al.*, 2005] and convection of ash [Raison *et al.*, 1985]. Changes in nutrient budgets expected soon after fire (first few years) arise from wind- and water-driven sediment export [Ewing, 1996; Huffman *et al.*, 2001; Whicker *et al.*, 2006], changes

in the physical properties of soil, such as hydrophobicity [Huffman *et al.*, 2001; MacDonald and Huffman, 2004; Martin and Moody, 2001], dissolution of ash [Chorover *et al.*, 1994], shifts in soil water pH [Murphy *et al.*, 2006b; Stephens *et al.*, 2004], changes in microbial biomass and activity [Mabuhay *et al.*, 2006; MacKenzie *et al.*, 2006; Yeager *et al.*, 2005], increased decomposition [Schoch and Binkley, 1986], and changes in biological demand for water and nutrients. Crown scorch, tree mortality, and stand replacement can affect canopy-related processes that are important in watershed balances of water and nutrients. These include interception of precipitation and cloudwater [Collett *et al.*, 1990; Friedland and Miller, 1999; Stottlemeyer and Troendle, 1999, 2001], scavenging of aerosols and gases [Hanson and Lindberg, 1991; Norby *et al.*, 1989; Nussbaum *et al.*, 1993], and transpiration. Enduring effects of fire on watershed balances (decade scale) relate ultimately to changes in vegetative cover. They include N-fixation and the accumulation of elements in aggrading plant biomass [Johnson *et al.*, 2005].

[3] In the Sierra Nevada, a century of fire suppression has resulted in fuel loads that exceed historical levels [Knapp *et al.*, 2005], has increased the potential for more severe crown fires [Keeley and Stephenson, 2000; Stephenson *et al.*, 1991], and has reduced opportunities for seedling recruit-

¹Marine Science Institute, University of California, Santa Barbara, California, USA.

²Department of Environmental Sciences, University of California, Riverside, California, USA.

³National Park Service, Inventory and Monitoring Program, Southwest Alaska Network, Katmai National Park and Preserve, King Salmon, Alaska, USA.

⁴Division of Natural Resources, Sequoia and Kings Canyon National Parks, Three Rivers, California, USA.

⁵Department of Ecology, Evolution, and Marine Biology and Donald Bren School of Environmental Science and Management, University of California, Santa Barbara, California, USA.

⁶U.S. Geological Survey, Western Ecological Research Center, Sequoia and Kings Canyon National Parks, Three Rivers, California, USA.

⁷Department of Ecology and Evolutionary Biology, University of California, Los Angeles, California, USA.

ment by some of the forest dominants [Keifer, 1998; Stephenson, 1996]. Alterations in fire regime are implicated in the decline of one of the more majestic Sierran trees, sugar pine (*Pinus lambertiana* Dougl.) [Van Mantgem et al., 2004]. In the late 1960s, the National Park Service began a program of prescription burning to reduce the hazardous fuel buildup and to restore fire to its former role in mixed conifer forests [Bancroft et al., 1985]. Tree ring studies indicate that from 1700 to 1900, natural fire return intervals in the region of Sequoia National Park averaged 10–20 years [Caprio and Graber, 2000], with mean return intervals as short as 3–8 years in groves of giant sequoia (*Sequoiadendron giganteum* [Lindl.] Buchh.) [Stephenson, 1999].

[4] The longevity of many postfire effects is poorly understood. Many studies follow changes in standing stocks, soil properties, nutrient fluxes (usually in soil), stream chemistry (less commonly), or runoff, for only a few months, or 2–3 years, after fire. Measurement of ecosystem outputs after fire using gauged streamflow is rare. Since restoring natural fire frequency is the goal of prescription burning in many forests, it is important to understand how watershed balances respond to fire on timescales that match target fire-return intervals.

[5] Here, we used a 16-year paired catchment study to investigate changes in watershed balances following prescribed fire in a mixed conifer forest in Sequoia National Park, California. Our goal was to examine whether fire-related changes in watershed balances persist as long as the proposed low-end natural fire-return interval in the park (~10 years [Swetnam et al., 1992]), and whether cumulative net export caused by fire could deplete nutrient stocks between successive fires. Inputs (wet + dry deposition) and outputs (gauged streamflow) of water and major ions (N , S , Cl^- , HCO_3^- , Ca^{2+} , Mg^{2+} , Na^+ , K^+ , H^+ , and SiO_2) were measured in paired headwater catchments in the Giant Forest region of the park for 7 years preceding, and 9 years following, the prescribed burning of one of the catchments. Cumulative fire-related export was compared to prefire standing stocks of key elements. To our knowledge, these results represent the longest uninterrupted record of the effects of prescribed fire on chemical fluxes from a gauged mixed conifer watershed in the western United States.

2. Methods

2.1. Site Description

[6] The study site consists of two adjacent headwater catchments located in the Giant Forest area of Sequoia National Park on the western slope of the southern Sierra Nevada, California ($36^\circ 34'\text{N}$, $118^\circ 44'\text{W}$, Figure 1). The smaller catchment (13.1 ha) is drained by Tharps Creek, an intermittent stream that generally flows from October to July. The larger catchment (49.8 ha) is drained by Log Creek, a perennial stream. Elevation ranges from 2097 to 2180 m in Tharps watershed and from 2158 to 2371 m in Log watershed. The region has a wet winter/dry summer Mediterranean climate. Mean January and July air temperatures in Giant Forest are 0°C and 18°C , respectively. Mean annual precipitation is approximately 100 cm [Williams and Melack, 1997a].

[7] Soils in both watersheds are predominantly humic lithic dystroxerepts and humic dystroxerepts [Soil Survey

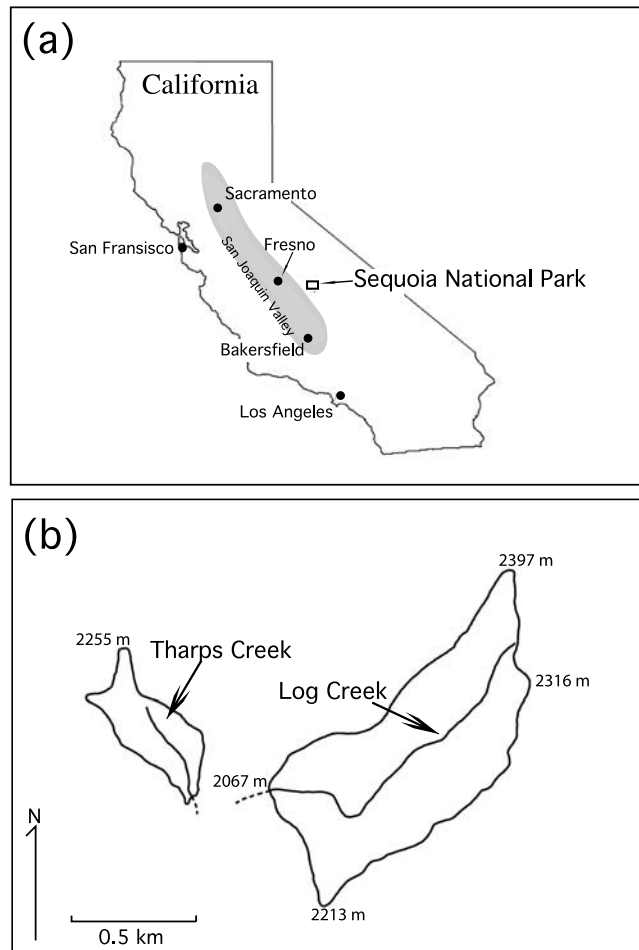


Figure 1. (a) Location of Sequoia National Park in California, United States, and (b) map of Tharps Creek and Log Creek watersheds ($36^\circ 34'\text{N}$, $118^\circ 44'\text{W}$) within the Giant Forest area of Sequoia National Park.

Staff, 2006] derived from granodiorite. They are typically <0.5 m deep, acidic, and well-drained [Halpin, 1995]. Rock outcrops make up about 3% of each watershed. Soils are moist from late fall through early summer from fall rains and snowmelt, and dry thereafter, although surface horizons may be moistened by infrequent summer thundershowers. Mean annual soil temperatures at a depth of 50 cm range from 8 to 10°C [Chorover et al., 1994].

[8] White fir (*Abies concolor* Lind. and Gord.) is the dominant species in both catchments. Subdominant tree species are giant sequoia, sugar pine, red fir (*Abies magnifica* A. Murr.), Jeffrey pine (*Pinus jeffreyi* Grev and Balf.), and incense cedar (*Calocedrus decurrens* [Torr.] Florin). Understory shrubs include green manzanita (*Arctostaphylos patula* Green), mountain whitethorn (*Ceanothus cordulatus* Kellogg), chinquapin (*Chrysolepis sempervirens* [Kellogg] Hjelm.), and gooseberry (*Ribes* spp.). The predominant groundcover is litter and duff.

2.2. Prescribed Burning of Tharps Watershed

[9] Tharps watershed was completely burned in a 14 ha prescribed fire ignited on October 23–26, 1990. Most of the fire was out by October 28, but pockets of ground fire

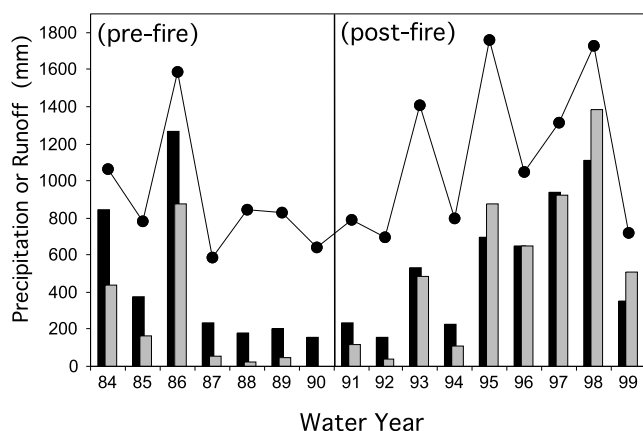


Figure 2. Annual precipitation (solid circles), and runoff for Log Creek (dark bars) and Tharps Creek (light bars). Median precipitation for 1984–1999 was 870 mm.

smoldered for several weeks. Ignitions occurred mostly during early evenings and into the night under a relative humidity of 30–40%. Fire behavior ranged from a backing fire with flame lengths of 0.05 to 0.15 m, and rates of spread up to 0.1 m min^{-1} , to a strip headfire with flame lengths of 0.6 to 2.4 m. Areas with heavy fuel concentrations and standing snags produced the highest flame lengths, occasionally torching nearby trees. Preburn surface fuel load was 210 Mg ha^{-1} ; fuel reduction was 85% [Mutch and Parsons, 1998]. Ash, initially 5–30 cm deep, was present in much of the catchment until the end of 1991 [Chorover *et al.*, 1994]. After the fire, sequoia, fir and pine seedlings were visible by the end of 1991, and fern species regenerated rapidly in the riparian zones [Williams and Melack, 1997b]. We found no records of fire in Tharps watershed prior to the introduction of prescription burning in 1991. Fire-scar dendrochronology studies from adjacent watersheds indicate that Tharps watershed and the control catchment (Log watershed) may not have burned for more than 120 years prior to our study (T. Caprio, personal communication).

2.3. Atmospheric Deposition

[10] Precipitation was monitored at a National Atmospheric Deposition Program (NADP) sampling station (NADP/NTN Monitoring Location CA75, Lower Kaweah) located approximately 4 km west of the study site at an elevation of 1902 m within the Giant Forest area of the Sequoia National Park. Samples for chemical analysis were collected weekly in accordance with NADP protocols in an Aerochem Metrics Model 201 sampler. The pH of unfiltered samples was measured at the park within 6 hours of collection. Precipitation samples were shipped to the NADP affiliated Central Analytical Laboratory at the University of Illinois at Champaign-Urbana for analysis of NO_3^- , SO_4^{2-} , Cl^- , NH_4^+ , Ca^{2+} , Mg^{2+} , Na^+ and K^+ . Filtered, refrigerated (2°C) subsamples from the Aerochem sampler were also sent to Michigan Technological University (1984 to 1989) or the Biogeochemistry Laboratory at the Rocky Mountain Forest and Range Experiment Station in Fort Collins, Colorado (1990 onward) for the same chemical analyses, described below for stream samples. Data from the Michigan or Colorado labs were used on six occasions when NADP chemistry data were missing for a particular month.

[11] Weekly precipitation was measured with a Belfort recording rain gauge at the same site. Belfort gauges may underestimate precipitation during snowfall [Tumbusch, 2003], thus precipitation may have been underestimated during winter months in our study. An additional Belfort weighing rain gauge, located 1 km southwest of the study site, at an elevation of 1992 m, was deployed from 1984 to 1986. Precipitation measured at this site was on average 9% ($\pm 4\%$ SD) higher per water year than that measured at the NADP site [Stohlgren *et al.*, 1991]. To account for this discrepancy, weekly precipitation volumes from the Belfort gauge at the NADP site were increased by 9% in the 16-year data set used in this study.

[12] Monthly volume-weighted mean (VWM) concentrations of solutes in Giant Forest precipitation were computed by the NADP. Monthly fluxes of solutes were calculated by multiplying VWM concentrations by the volume of precipitation and then normalizing the product to watershed area. Annual solute fluxes were obtained by summation for each water year, defined as beginning October 1 and ending September 30, and referred to by the calendar year in which they ended. Unless otherwise noted, all years indicated herein refer to water years. Annual VWM concentrations of solutes in wet deposition were obtained by dividing annual fluxes by annual precipitation volumes.

[13] Dry deposition of HNO_3 and SO_2 vapor, and particulate NO_3^- , SO_4^{2-} , NH_4^+ , Ca^{2+} , Mg^{2+} , Na^+ and K^+ , was measured at the Wolverton Meadow (2250 m) dry deposition station located 3.5 km from the study catchments (Figure 1). The station was part of the NOAA-operated AIRMoN dry-deposition network [Hicks *et al.*, 1991; Meyers *et al.*, 1991]. The Dry Deposition Inferential Method (DDIM) used at the Wolverton station used airborne chemical concentrations and the deposition velocity of individual chemical species to compute dry deposition rates [Meyers *et al.*, 1998]. Ambient air concentrations of major elements and compounds were determined by a filter-pack accumulating system that was sampled about every seven days. Sequential filters removed particles $< 2 \mu\text{m}$ (Teflon), HNO_3 vapor (nylon), and SO_2 vapor (treated cellulose), after air passage through a slightly heated elutriator. Deposition velocities were derived from a semi-empirical model that used site-specific meteorological data and time-varying information about surface conditions. The Wolverton DDIM model was parameterized to grass and Ponderosa/Lodgepole Pine. Owing to the model's reliance on leaf-area index, it is likely that dry deposition rates at the vegetated Wolverton station are similar to rates at the study catchments.

2.4. Stream Discharge and Chemistry

[14] Stream discharge was measured year-round using 0.3 m and 0.08 m Parshall flumes for Log and Tharps creeks, respectively. The flumes were equipped from 1984 to 1990 with Stevens Type-F strip chart recorders. Strip charts were summarized manually to obtain daily discharge. In 1990 and 1991, Stevens Type A/F electronic data loggers were installed at Log and Tharps creeks. Annual discharge volumes derived from daily mean stage height recorded on strip charts were comparable to those derived from data loggers ($\pm 5\%$). When gaps in the record occurred (due to equipment malfunction), discharge was estimated by linear

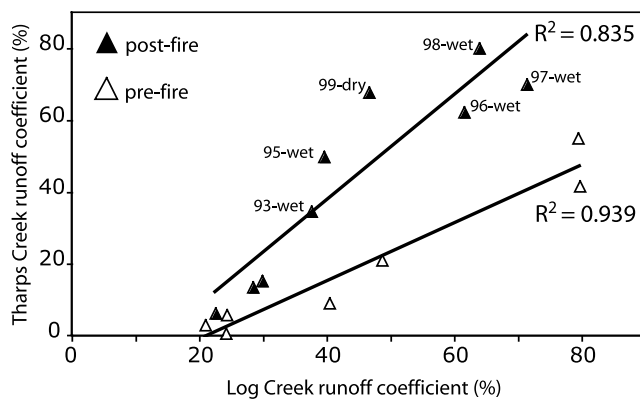


Figure 3. Relationship between runoff coefficients (% precipitation) for Tharps Creek and Log Creek for prefire years (1984–1990, open symbols) and postfire years (1991–1999, solid symbols). Selected postfire years are designated as “dry” or “wet” depending on whether below- or above-median precipitation occurred that year, using the median precipitation for water years 1984–1999 (870 mm). Regression lines were significant ($p < 0.05$). Slopes of the regression lines were significantly different ($p < 0.05$).

interpolation, using the last known discharge before, and the first known discharge after, the gap.

[15] Water samples were taken year-round in Log Creek and during all periods of flow in Tharps Creek, which was generally from October through June or July, except during drought years when flow sometimes ceased during May. During prefire years, stream samples were collected every 2 weeks in both catchments immediately upstream of the flumes. Postburn stream flow was sampled daily from March 3 to April 10, 1991, and weekly during the remaining snowmelt period of 1991, and during 1992 and 1993.

During 1994 and 1995, streams were sampled approximately every 2 weeks, and from 1996 to 1999, once per month. Samples were collected in acid-washed polyethylene bottles that were rinsed several times with distilled, deionized water and prerinsed with sample water. Unfiltered stream water samples were analyzed for pH and acid neutralizing capacity (ANC) within 6 hours of collection. An Altex model 3500 pH meter with a Beckman glass body probe for dilute water was used from 1984 to August 1990, and was subsequently replaced by a Beckman model pH 40. ANC was determined by titration [Gran, 1952], which was performed with NIST-traceable 0.1 N HCl in an open beaker on quiescent samples between pH 4.5 and 3.5. Filtered samples were stored at 4°C prior to colorimetric analysis for SiO_2 (silicomolybdate method [Strickland and Parsons, 1972]) and NH_4^+ (indophenol blue method [APHA, 1981]) at Sequoia National Park. From 1984 to 1989, filtered samples were refrigerated at 2°C and shipped to Michigan Technological University for analyses of NO_3^- , Cl^- , SO_4^{2-} , and base cations. From 1990 to the end of the study, samples for the latter analyses were shipped to the Biogeochemistry Laboratory at the Rocky Mountain Forest and Range Experimental Station in Ft. Collins, Colorado. During both periods, samples were analyzed within 40 days of collection on an automated Dionex 2020 ion chromatograph according to methods and QA/QC procedures detailed by Stottlemeyer and Troendle [1987] and Stottlemeyer [1987]. Total dissolved nitrogen (TDN) was determined by the Valderrama [1981] method in 1994 and 1995 only. Filtered water samples were digested with a NaOH-persulfate oxidizing reagent under high heat (260°C) and pressure which converted all N forms to nitrate, which was then quantified on a Lachat autoanalyzer. Dissolved organic N (DON) was computed as the difference between TDN and dissolved inorganic N ($\text{NH}_4^+ + \text{NO}_3^-$, or DIN).

Table 1. Mean Annual Inputs (Wet and Dry Deposition) and Outputs (Stream Export), and Mean Annual VWM Concentrations of Major Ions in Precipitation (Giant Forest) and Streamflow (Log Creek) for Water Years 1984–1999^a

	kg ha ⁻¹ yr ⁻¹			VWM Concentration, $\mu\text{mol L}^{-1}$			
	Atmospheric Deposition			Stream Export ^b	Watershed Balance	Precipitation	Stream-flow
	Wet	Dry	Total				
NO_3^- -N	1.199	1.242 ^{c,d}	2.441	0.004	2.437	9.1	0.1
NH_4^+ -N	1.394	0.077 ^d	1.471	0.012	1.459	10.7	0.1
Inorganic N	2.593	1.319 ^e	3.912	0.016	3.896	19.7	0.2
DON ^f	—	—	—	3.355	—	—	—
Cl^-	1.163	0.032	1.195	2.031	-0.836	3.3	12.0
SO_4^{2-} -S	0.933	0.199 ^g	1.132	0.356	0.776	3.0	2.2
HCO_3^-	—	—	—	86.4	—	—	293.0
H^+	0.036	0.105 ^h	0.130	0.001	0.129	3.3	0.2
Ca^{2+}	0.469	0.016	0.485	17.379	-16.894	1.3	91.1
Mg^{2+}	0.131	0.007	0.138	2.448	-2.310	0.6	19.4
K^+	0.192	0.023	0.215	4.133	-3.918	0.5	21.5
Na^+	0.768	0.021	0.789	14.713	-13.924	3.4	134.8

^aWatershed balances are mean inputs-mean outputs. Positive balances indicate net retention; negative balances indicate net export.

^bValues for the control catchment, Log Creek watershed.

^cIncludes HNO_3 -N.

^d HNO_3 -N was overestimated, and NH_4^+ -N underestimated, by the AIRMoN sampler [see Meyers *et al.*, 1991].

^eDoes not include NH_3 , NO_2 , HNO_2 , and NO (see text).

^fMean values for 1994–1995.

^g $\text{SO}_2 + \text{SO}_4^{2-}$, approximately 59% is SO_2 .

^hCalculated assuming complete conversion of deposited SO_2 to H_2SO_4 , following Lindberg *et al.* [1986].

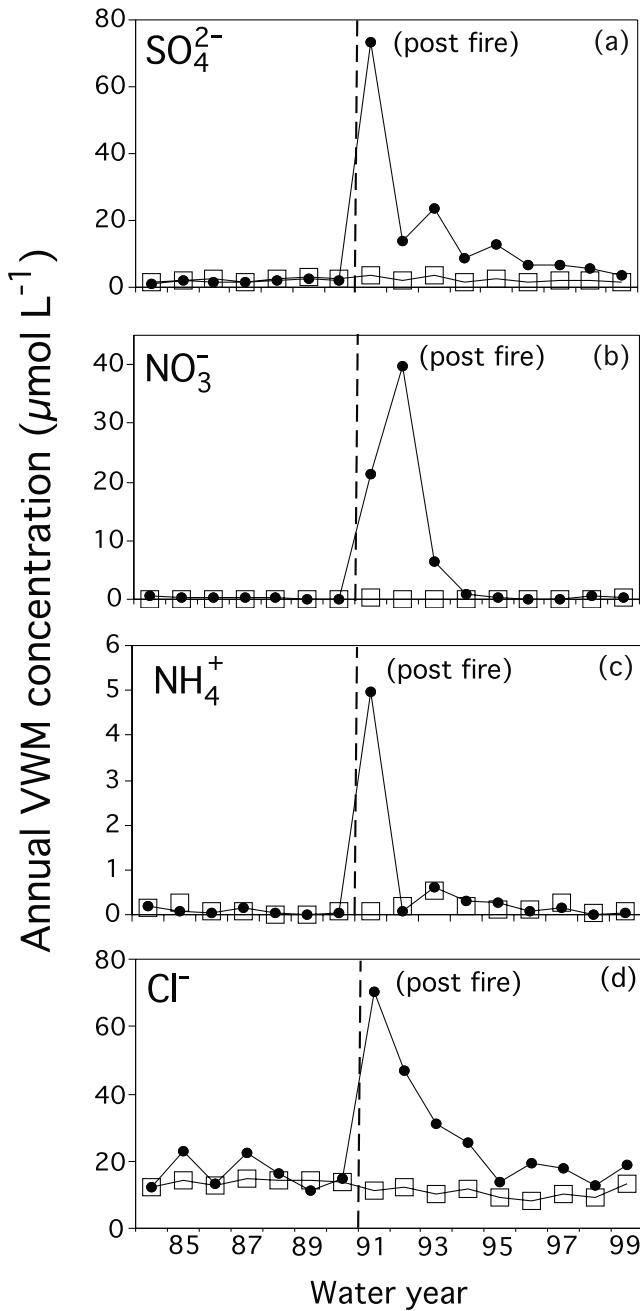


Figure 4. Annual volume weighted mean (VWM) concentrations of (a) SO_4^{2-} , (b) NO_3^- , (c) NH_4^+ , and (d) Cl^- in Log Creek (squares) and Tharps Creek (circles) for water years 1984–1999. The prescribed burn in Tharps Creek watershed occurred in October 1991.

[16] Annual volume-weighted mean solute concentrations (VWM) were calculated for stream outflow according to the following equation:

$$C_{\text{vwm}} = \frac{\sum_{i=1}^n C_i V_i}{\sum_{i=1}^n V_i} \quad (1)$$

where C_{vwm} is volume-weighted mean solute concentration (mol m^{-3}), n is number of outflow samples during the year, C_i is solute concentration for sample i (mol m^{-3}), and V_i is water flux associated with sample i (m^3).

[17] Assigning volumes to outflow chemistry was complicated since discharge was computed on a daily time step, but chemical samples were collected less frequently. We used a modification of the period weighting procedure to distribute discharge to chemical samples [Coats and Goldman, 2001]. Period-weighting is superior to the ratio-estimator method in snowmelt dominated systems provided there are adequate chemical samples. In our methodology, chemistry from a stream sample was applied to the discharge over an interval including that day and bounded by the midpoints between the preceding and following samples. The midpoint rule was superseded if a hydrologic event of sufficient magnitude (i.e., rainfall that increased streamflow, freezing events that abruptly decreased streamflow, and the initiation of snowmelt runoff) occurred between sample dates. For these situations, date of the event was used as the division and chemistry from the later sample was used with streamflow on the day of the event. No attempt was made to interpolate stream chemistry between sampling dates because day to day variations in stream chemistry were usually small in relationship to changes in discharge. Annual solute export was calculated as the product of annual outflow discharge and C_{vwm} , normalized by catchment area.

[18] Regression analysis (analysis of covariance, or ANCOVA, following Grabow *et al.* [1998]) was used with the paired watershed data to determine whether prescribed fire had a significant effect on area-weighted net annual catchment export of water and major ions. The underlying regression model is given by (2) and (3),

$$Y_1 = \beta_0 + \beta_1 X_1 + \epsilon' \quad (2)$$

$$Y_2 = (\beta_0 + \beta_2) + (\beta_1 + \beta_3) X_2 + \epsilon' \quad (3)$$

where Y_1 and X_1 are net annual catchment outputs from the treatment (Tharps) and control (Log) watersheds, respectively, during the calibration (prefire) period, Y_2 and X_2 are net annual catchment outputs of water or solutes from the treatment and control watersheds during the treatment (postfire) period, β_0 and β_1 are the calibration period intercept and slope, β_2 and β_3 are the adjustments to the intercept and slope for the treatment period, and ϵ' is the independent noise term.

3. Results

3.1. Precipitation and Runoff

[19] From 1984 to 1999, annual precipitation ranged from 588–1758 mm. Mean and median annual precipitation were 1141 mm and 870 mm, respectively. Six consecutive years with below median precipitation occurred in the middle of the study (Figure 2). The study period was preceded by 2 years with high precipitation, including the strong El Niño year of 1983, which resulted in 2266 mm of precipitation. One other strong El Niño year (1998) occurred toward the end of the study period. Most precipitation occurred during

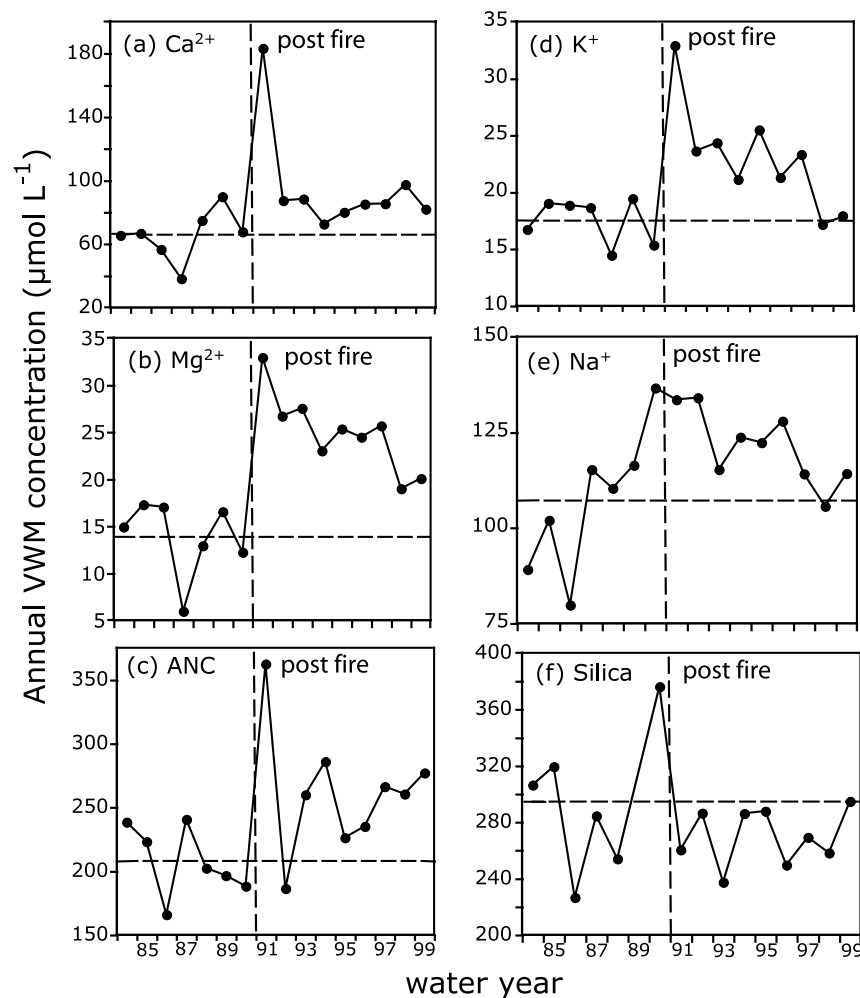


Figure 5. Annual volume weighted mean (VWM) concentrations of (a) Ca^{2+} , (b) Mg^{2+} , (c) acid neutralizing capacity (ANC), (d) K^{+} , (e) Na^{+} , and (f) silica in Tharps Creek from 1984 to 1999. Dashed horizontal lines are prefire averages (1984–1990).

winter months, about half as snow and half as rain. Snowmelt usually occurred from March to May.

[20] Runoff volumes were affected by the large interannual variation in precipitation during our study, which included a 6-year drought during 1987–1992 (Figure 2). Mean annual runoff in Log watershed during the drought was 29% of precipitation; excluding drought years, mean annual runoff was 56% of precipitation. Antecedent years had a clear effect on runoff. Wet years (with above median precipitation) preceded by other wet years produced the highest runoff coefficients (67–80%). Dry years (with below median precipitation) preceded by other dry years produced the lowest runoff coefficients (23–33%). Before fire, runoff coefficients in Tharps watershed were consistently lower than in Log watershed, averaging 51% during wet years, and 8% during dry years.

[21] Runoff was significantly higher after fire in Tharps watershed. Both before and after the fire, runoff coefficients in Log and Tharps watersheds were significantly correlated, but the slope of the postfire regression equation was significantly higher (Figure 3). Before the burn, measurable flow occurred in Tharps Creek for an average of 195 days yr^{-1}

(all years), or 150 days yr^{-1} if only dry years are considered. After the burn, these values increased to 255 days yr^{-1} and 225 days yr^{-1} , respectively [Moore and Keeley, 2000]. The immediate effect of fire on discharge was mitigated to some degree by the drought, which continued for 2 years after the fire. Three of the first four years after the fire (1991, 1992, 1994) were dry years (Figure 2), and runoff from the burned catchment during those years was on average 7% higher than that predicted by the prefire relationship. During wetter postfire years, the burnt catchment produced an average of 35% more runoff than predicted. Nine years after the burn, there was no evidence that runoff in Tharps watershed was returning to prefire levels (Figure 3).

3.2. Atmospheric Loading

[22] NH_4^+ and NO_3^- contributed the majority of annual solute flux in wet deposition, followed by H^+ , Cl^- , Na^+ and SO_4^{2-} , which were delivered annually in similar quantities (molar basis) (Table 1). Annual VWM pH averaged 5.49. Dry deposition consisted mostly of HNO_3 , NO_3^- , NH_4^+ , SO_2 and SO_4^{2-} , contributing about 18% and 34% of annual loadings of S and inorganic N, respectively (Table 1). Dry

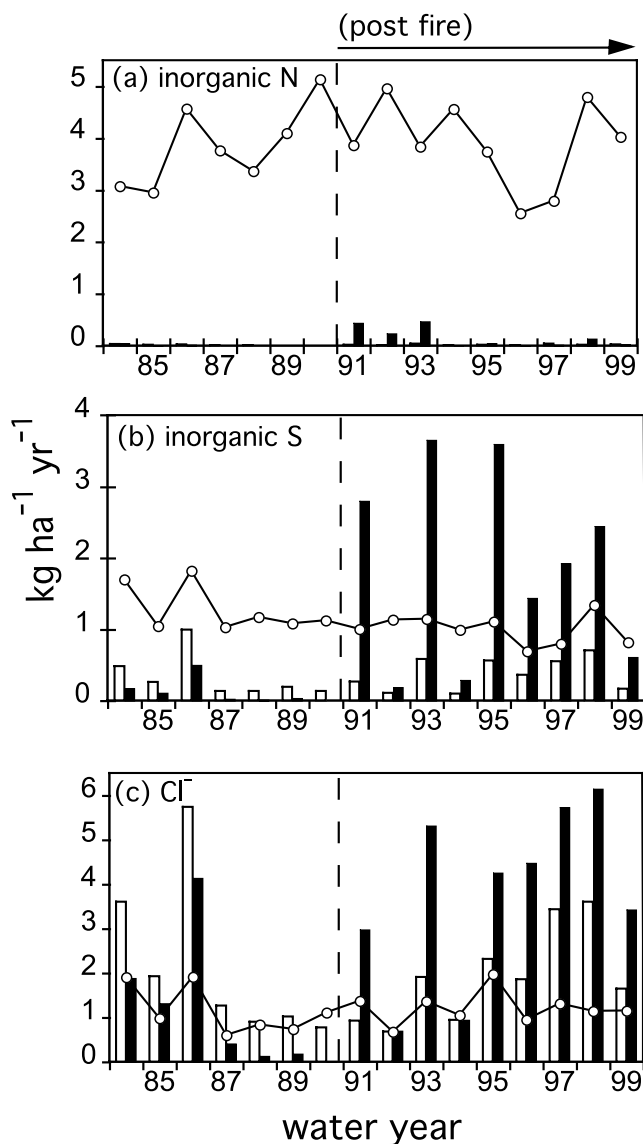


Figure 6. Annual atmospheric inputs (open circles) and catchment outputs for Log Creek watershed (open bars) and Tharps Creek watershed (solid bars) for water years 1984–1999 for (a) inorganic N, (b) inorganic S, and (c) Cl^- . Atmospheric inputs are wet + dry deposition.

deposition contributed 3–4% of atmospheric loading of Ca^{2+} , Mg^{2+} , and Na^+ , somewhat more in the case of K^+ (11%, Table 1). The AirMon filtration device used for collection was not designed for coarse particles ($>2 \mu\text{m}$), hence, the true contribution of dry deposition to base cation inputs may be higher in Giant Forest than we estimate.

3.3. Stream Chemistry

[23] The dominant ions in streamflow were HCO_3^- , Na^+ , Ca^{2+} and (Table 1). Based on mean annual VWM concentrations, base cations occurred in stream water in the order $\text{Na}^+ > \text{Ca}^{2+} \gg \text{K}^+ > \text{Mg}^{2+}$, strong acid ions in the order $\text{Cl}^- > \text{SO}_4^{2-} > \text{NO}_3^-$ (for both, molar basis). Mean annual VWM pH in Log Creek was 6.74. DIN was normally near or below detection in both creeks, although brief pulses were observed during snowmelt.

[24] Solute concentrations increased in Tharps Creek after the fire. Annual VWM $[\text{NH}_4^+]$ declined to the prefire baseline in the second year after fire (1992, Figure 4), but climbed again slightly during 1993, which was the first wet year after the fire (Figure 2). Annual VWM $[\text{NO}_3^-]$ peaked during the second postfire year (Figure 4), and returned to baseline levels by the fifth postfire year. The other strong acid anions (SO_4^{2-} and Cl^-) were higher in Tharps Creek for several years after fire (Figure 4). Annual VWM $[\text{Cl}^-]$ returned to prefire levels in Tharps Creek after 4 years; annual VWM $[\text{SO}_4^{2-}]$ in Tharps Creek was still above the prefire baseline 9 years after fire (Figure 4). Sufficient ANC was produced after fire to neutralize inputs of strong acids; the pH of Tharps Creek was similar before (6.7) and after (6.9) the fire.

[25] The postfire pulse of strong acid anions in Tharps Creek (Figure 4) was accompanied by an even larger pulse of base cations, which was dominated by Ca^{2+} (on a molar basis) during the first snowmelt season following the fire (Figure 5). At the end of the study, annual VWM mean $[\text{Mg}^{2+}]$ was still declining from its postfire maximum; annual VWM means for $[\text{Na}^+]$ and $[\text{K}^+]$ declined to the prefire baselines by the eighth year after the fire (Figure 5). Interannual variation in annual VWM $[\text{SiO}_2]$ in Tharps Creek over the course of the study did not follow a pattern related to fire (Figure 5).

3.4. Mass Balances

[26] Absent disturbance, we observed almost complete retention of inorganic N inputs (Figure 6). On average, annual export of DIN from the control catchment was $<1\%$ of annual inputs of inorganic N (Table 1). Despite increased export of DIN for 3 years after fire (Figure 4), net retention of inorganic N was observed in Tharps watershed throughout the postfire period (Figure 6). By the fourth year after the burn, N export from Tharps declined to a level consistent with the prefire relationship between N export from the paired catchments (Figure 8).

[27] Absent disturbance, atmospheric deposition accounted for only a small fraction of base cation export in most years (Figure 7). Averaged over the study, stream export in the control catchment exceeded atmospheric loading of Ca^{2+} , Mg^{2+} , Na^+ and K^+ by factors of 35, 18, 19 and 19, respectively (Table 1). Prescribed fire had a long-lived effect on base cation export. Before the fire, base cation export per unit area was greater in Log watershed than Tharps. After fire, area-weighted output of base cations in Tharps was roughly the same, or exceeded, that in Log watershed (Figure 7). Annual export of base cations from Tharps watershed was significantly correlated to export from Log watershed both before and after the fire (Figure 9). However, enhanced export from Tharps watershed significantly increased the slopes of the regression equations for all species after fire (Figure 9).

[28] The prescribed burn altered watershed balances of SO_4^{2-} and Cl^- . In undisturbed forest, net retention of inorganic S was always observed. Atmospheric inputs of S exceeded stream export of SO_4^{2-} S in the control watershed by an average factor of three (Figure 6); S accumulated in the ecosystem at the rate of $0.8 \text{ kg S ha}^{-1} \text{ yr}^{-1}$ (Table 1). Chloride balances were more variable from year to year, but the cumulative net export ($0.014 \text{ kg Cl}^- \text{ ha}^{-1}$) in Tharps

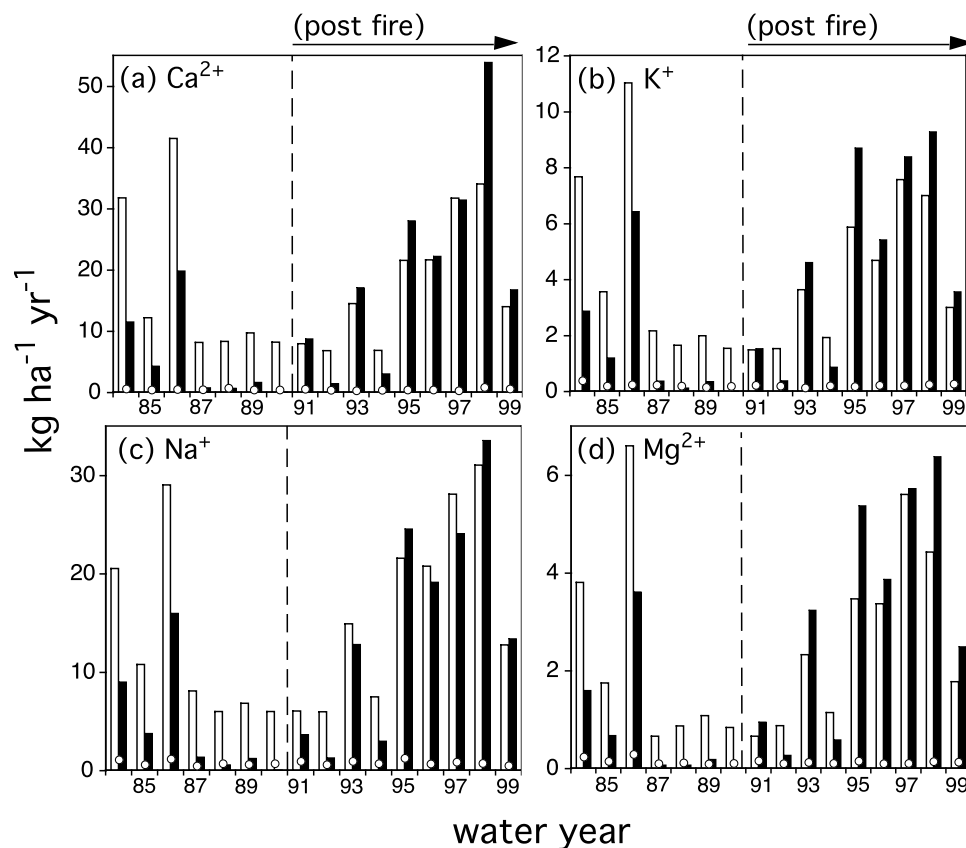


Figure 7. Annual atmospheric inputs (open circles) and catchment outputs for Log Creek watershed (open bars) and Tharps Creek watershed (solid bars) for water years 1984–1999 for (a) Ca^{2+} , (b) K^+ , (c) Na^+ , and (d) Mg^{2+} . Atmospheric inputs are wet + dry deposition.

watershed during the prefire period was close to zero (Figure 6). After fire, export of both S and Cl^- in Tharps watershed well exceeded atmospheric inputs every year except 1992 and 1994, which were dry years with little discharge in Tharps Creek (Figure 6). For Cl^- , this change produced a postfire regression equation for the paired watersheds with a significantly higher intercept (Figure 8) and a cumulative net loss of $23 \text{ kg Cl}^- \text{ ha}^{-1}$ (Table 2). After fire, SO_4^{2-} losses from the burned catchment were no longer correlated to losses from the control catchment (Figure 8). Sulfate export from the burned catchment was especially high during the first postfire year (1991) and during wet postfire years (1993, 1995–1998). As late as 1999 (a dry year), annual export of SO_4^{2-} from Tharps watershed was still twice as high as that predicted by export from the control catchment (Table 2).

4. Discussion

4.1. Effects of Fire on Watershed Balances

[29] Increases in runoff following fire are attributable to several processes, including decreased interception and evapotranspiration, decreased infiltration, and the development of a water-repellent layer at or near the soil surface [Cerde, 1998; Helvey, 1980; Lavabre *et al.*, 1993; McNabb *et al.*, 1989; Prosser and Williams, 1998; Robichaud, 2000; Robichaud and Waldrop, 1994]. Fire-induced hydrophobicity has been shown to persist in soils up to 2 years at some sites

[Huffman *et al.*, 2001]. Given the intensity of the prescribed fire in Tharps watershed, it seems reasonable to attribute some of the increased runoff after fire to changes in soil properties, at least early on. However, differences in water yield between the burned and unburned catchment were more pronounced during the last 2 years of the study (1998, 1999) than in years closer to the burn (Figure 2).

[30] The prolonged increase in water yield we observed after fire is consistent with observed tree mortality. Prefire mean annual tree mortality (1986–1990) was $<1\%$; this increased to 17.2% after fire (1991–1995) [Mutch and Parsons, 1998]. Between 1989 and 1994, 75% of trees $\leq 50 \text{ cm}$ diameter-at-breast-height (dbh), and 25% of trees $> 50 \text{ cm}$ dbh, died in Tharps, and only three ingrowth trees were observed [Mutch and Parsons, 1998]. Crown scorch was the predominant cause of mortality. Trees continued to die in Tharps as a consequence of the burn into the late 1990s (L. Mutch, personal communication). Crown scorch and tree death could have decreased interception of rain and snow by the canopy in the burned catchment. Interception rates reported from other conifer forests range from 20% to 40% of precipitation [Blew *et al.*, 1993; Fahey *et al.*, 1988; Friedland and Miller, 1999; Stottlemeyer and Troendle, 1999, 2001]. However, mean throughfall event depths were not statistically different between burned and unburned plots at our study site during the first 2 years after fire, which were dry years

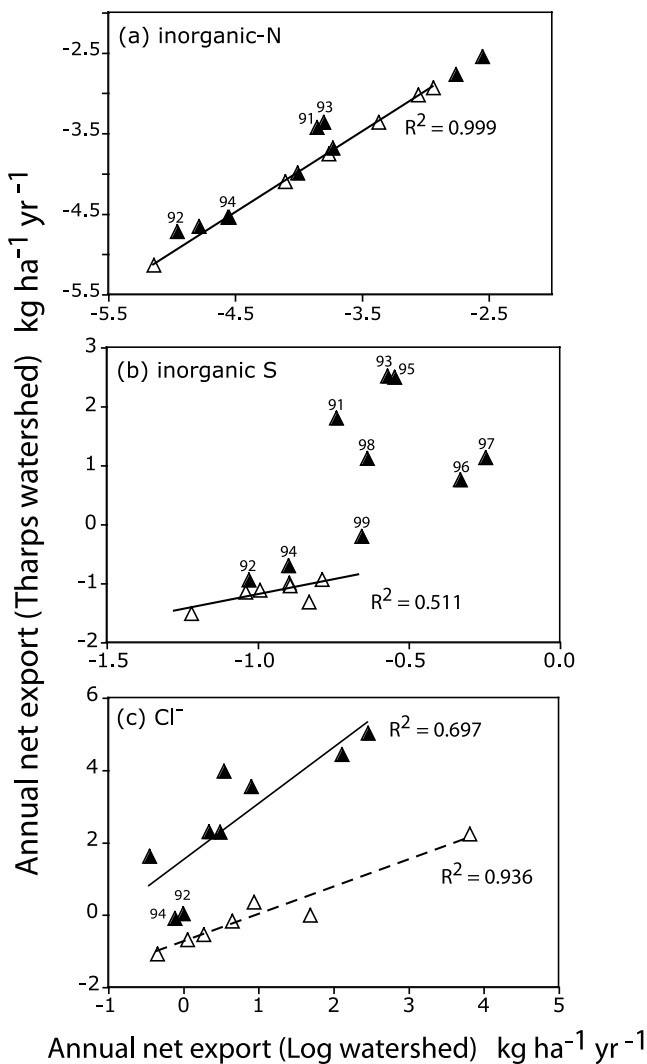


Figure 8. Relationships between annual net export from Tharps watershed and Log watershed for (a) inorganic N, (b) inorganic S, and (c) Cl⁻, during prefire years (1984–1990, open symbols) and postfire years (1991–1999, solid symbols). Net export <0 indicates net watershed retention. All regression lines are significant ($p < 0.05$). Regression lines shown in Figures 8a and 8b are for prefire data only. The intercepts (but not the slopes) of the prefire and postfire regression equations for Cl⁻ in Figure 8c were significantly different ($p < 0.05$). Years are indicated above selected postfire data.

(J. Chorover, unpublished data). We lack throughfall volumes for other postfire years.

[31] Several potential N inputs were not included in our catchment balances. These include unmeasured N species in dry deposition (NH₃, NO₂, HNO₂, and NO), which collectively can amount to as much as 71% of airborne N in summer months [Bytnerowicz *et al.*, 2002], direct stomatal uptake of NH₃ and NO₂ [Hanson and Lindberg, 1991; Norby *et al.*, 1989; Nussbaum *et al.*, 1993], cloudwater interception [Collett *et al.*, 1990], and deposition of atmospheric organic N [Sickman *et al.*, 2001]. Throughfall N fluxes measured at the site using bulk collectors (6–11 kg N

ha⁻¹ yr⁻¹ [Chorover *et al.*, 1994]) and ion exchange resin columns (11.6 kg N ha⁻¹ yr⁻¹ [Fenn *et al.*, 2003]) were higher than our estimate for inorganic N loading (3.9 kg N ha⁻¹ yr⁻¹). Net canopy retention of N, ranging from 30% to 70% of atmospheric deposition, is expected in conifer forest [Fenn *et al.*, 2000; Friedland and Miller, 1999; Lindberg *et al.*, 1986; Stottlemeyer and Troendle, 2001]. Hence, the true deposition rate for N in Giant Forest is probably even higher than reported throughfall fluxes.

[32] The net effect of prescribed fire on watershed balances of inorganic N was small. The largest annual output in Tharps (0.47 kg N ha⁻¹, in 1993) was only 12% of atmospheric inputs that year. Given that our N inputs were underestimated, the true percentage is even smaller. Cumulative postfire export of N from 1991 to 1999 (1.4 kg N ha⁻¹) was smaller than atmospheric deposition of N in the first year after the fire alone (4.9 kg N ha⁻¹). However, volatilization of N during the fire was an unmeasured output in the burned catchment. Volatilization losses of N at three burned mixed-conifer sites in the eastern Sierra Nevada ranged 56–362 kg N ha⁻¹ [Caldwell *et al.*, 2002]. Replacement times for this much N would range from 14 to 93 years at our site, if supplied by wet + dry deposition (present study), or 5 to 30 years to replace, if supplied by throughfall (using rate reported by Fenn *et al.* [2003]). Replacement of N stocks after fire is also affected by whether fire results in stand replacement, and whether postfire colonizers fix N. In the eastern Sierra Nevada, replacement of a Jeffrey pine forest with shrubland dominated by the N-fixer *Ceanothus velutinus* Dougl. resulted in N inputs (10–40 kg N ha⁻¹ yr⁻¹) that exceeded atmospheric deposition of N in the area [Johnson *et al.*, 2005]. Although an actinorhizal shrub (*C. cordulatus* Kellogg [Oakley *et al.*, 2003]) occupies the understory at our site, prescribed fire did not result in stand replacement.

[33] The 2 years of DON data we have from the control catchment suggest that the majority (>99%) of total N export at our site occurs as DON (Table 1). Average export of DON in Log watershed during 1994–1995 was 3.4 kg N ha⁻¹ yr⁻¹; mean annual inorganic N loading during the same period was 4.2 kg N ha⁻¹ yr⁻¹. Hence, as much as 80% of inorganic N inputs in undisturbed forest at our site may be balanced by organic N outputs. We do not know how fire affected DON export at the site.

[34] Inorganic N reaching Tharps Creek after fire likely resulted from leaching of ash, decreased plant uptake, and changes in microbial activity. Net N mineralization can increase in forest soil after burning [Kaye and Hart, 1998; Knoepp and Swank, 1995; Schoch and Binkley, 1986; White, 1986] and may be accompanied by increases in net nitrification [Fuller *et al.*, 1987; Kaye and Hart, 1998]. Nitrate export in forests following fire may also result from decreased microbial uptake of NO₃⁻ [Kaye and Hart, 1998]. Recovery time for NO₃⁻ in streams following fire is commonly 3 years or less [Bayley *et al.*, 1992; Carignan *et al.*, 2000].

[35] Concentrations of NO₃⁻ in soil solution [Chorover *et al.*, 1994] and stream water (the latter, volume weighted) were highest in Tharps Creek during the second snowmelt season following fire (Figure 4). This pattern suggests a delay in the processes responsible for producing NO₃⁻ after fire, or for releasing it to drainage waters. Lags in net NO₃⁻ production have been observed after disturbance in conif-

Table 2. Observed Versus Predicted Annual Net Export ($\text{kg ha}^{-1} \text{ yr}^{-1}$) of Solutes in Tharps Creek in Postfire Years^a

Year	Calcium Net Export			Magnesium Net Export			Sodium Net Export			Potassium Net Export		
	Obs.	Predict.	Δ	Obs.	Predict.	Δ	Obs.	Predict.	Δ	Obs.	Predict.	Δ
91	8.2	0.1	8.1	0.8	-0.2	1.0	2.7	-0.5	0.8	1.3	-0.3	1.6
92	1.1	-0.4	1.5	0.2	0.0	0.2	0.7	-0.3	0.2	0.2	-0.3	0.4
93	16.9	3.8	13.1	3.1	0.8	2.3	11.9	5.3	3.6	4.5	1.1	3.4
94	2.7	-0.4	3.1	0.5	0.1	0.4	2.3	0.6	0.7	0.7	0.0	0.7
95	27.6	7.5	20.1	5.2	1.5	3.8	23.3	9.4	8.2	8.5	2.4	6.1
96	21.8	7.5	14.3	3.8	1.4	2.3	18.5	9.3	7.3	5.2	1.7	3.5
97	31.2	13.0	18.1	5.6	2.7	2.9	23.3	13.9	7.3	8.2	3.5	4.7
98	53.1	14.0	39.1	6.2	2.0	4.2	32.9	15.9	8.8	9.0	3.1	5.9
99	16.2	3.4	12.9	2.4	0.5	1.9	12.9	4.2	4.2	3.3	0.6	2.7
Σ	178.8	48.5	130.3	27.8	8.9	18.9	128.5	57.9	70.6	40.9	11.9	29.0

Year	Inorganic N Net Export			Sulfate-S Net Export			Chloride Net Export			Silicon Export ^b		
	Obs.	Predict.	Δ	Obs.	Predict.	Δ	Obs.	Predict.	Δ	Obs.	Predict.	Δ
91	-3.43	-3.85	0.42	1.8	-1.0	2.7	1.6	-1.1	2.7	8.7	3.0	5.8
92	-4.72	-4.96	0.23	-0.9	-1.2	0.3	0.0	-0.8	0.8	3.4	-0.9	4.3
93	-3.37	-3.80	0.43	2.5	-0.8	3.3	4.0	-0.4	4.3	32.3	15.8	16.5
94	-4.54	-4.55	0.01	-0.7	-1.1	0.4	-0.1	-0.8	0.7	8.5	2.8	5.8
95	-3.69	-3.72	0.04	2.5	-0.8	3.3	2.3	-0.5	2.8	70.7	33.1	37.6
96	-2.55	-2.54	-0.01	0.8	-0.5	1.3	3.5	-0.1	3.6	45.7	26.1	19.6
97	-2.77	-2.75	-0.02	1.1	-0.5	1.6	4.4	0.8	3.6	69.6	41.9	27.6
98	-4.66	-4.78	0.13	1.1	-0.8	2.0	5.0	1.1	3.9	100.3	55.3	45.0
99	-4.00	-4.00	0.01	-0.2	-0.9	0.7	2.3	-0.4	2.7	42.3	12.8	29.6
Σ	-33.73	-35.00	1.23	7.9	-7.6	15.5	23.0	-2.1	25.2	381.4	189.8	191.6

^aPredicted export was obtained using net export values from Log watershed from postfire years in the regression equations relating prefire net export from Tharps watershed with that from Log watershed (Figures 8 and 9). Negative values indicate net watershed retention. The difference between observed and predicted values (Δ) represents enhanced catchment export resulting from pools and processes established after fire. Cumulative values for the period 1991–1999 (Σ) are at the bottoms of the columns. Values in bold type are estimates of cumulative net export after 9 years that resulted from postfire processes, expressed as kg ha^{-1} .

^bAtmospheric inputs of silica were not measured in the study; values are for total annual export.

erous forests, grasslands, and shrublands, and are sometimes attributed to delayed responses by nitrifying bacteria to NH_4^+ availability [Gerla and Galloway, 1997; Vitousek et al., 1982; Wan et al., 2001; Wright and Hart, 1997]. This explanation is supported by the rapid recovery of $[\text{NH}_4^+]$ to prefire levels in soil solution [Chorover et al., 1994] and stream water (present study) observed during the second postfire year (Figure 4).

[36] Prolonged changes in base cation yield following fire, such as we observed, are not widely reported. This may be an artifact of study design. Excluding studies of burned logging slash, few studies of prescribed burns in conifer forest provide information about base cation export; existing reports are for stream concentrations rather than catchment fluxes. After a prescribed fire of similar intensity in mixed conifer forest at similar elevation in the Lake Tahoe Basin, Stephens et al. [2004] observed somewhat higher Ca^{2+} , Mg^{2+} and K^+ concentrations in ephemeral streams, compared to control areas, over the course of one water year. Bech et al. [2005] observed short-lived inputs (<1 year) of Ca^{2+} and Mg^{2+} in a Sierra Nevada stream after prescribed fire. However, base cation concentrations in stream water remained higher for at least 9 years following fire in a Canadian Shield catchment [Bayley et al., 1992].

[37] One interpretation of persistently higher export of SiO_2 and ANC (mostly HCO_3^-) in Tharps watershed after fire is that weathering rates were higher (Figure 10). Both before and after fire, ion rankings in streamflow were generally consistent with ion yields expected from the weathering of plagioclase feldspars in granite [Melack and

Stoddard, 1991; Williams et al., 1993]. However, Si fluxes between plants and soil, and accumulation of biogenic opal in the forest floor, can be in the same order of magnitude as stream export of Si [Derry et al., 2005; Markewitz and Richter, 1998; Sommer et al., 2006]. Decreases in biosequestration of Si after fire, and dissolution of biogenic silica, should explain some of the postfire export of SiO_2 observed in Tharps watershed. Based on export from the control catchment, cumulative export of Si from Tharps watershed during the postfire period was twice as high as predicted (Table 2). In contrast, observed cumulative net export of Ca^{2+} , Mg^{2+} , Na^+ and K^+ from Tharps watershed was higher than predicted by factors of 5, 5, 3, and 6, respectively, during the postfire period (Table 2). Apparently, postfire processes accelerated catchment losses of base cations to a greater degree than SiO_2 losses. In addition to any increases in weathering, these processes likely included dissolution of ash [Chorover et al., 1994], remineralization, decreases in plant uptake, and alteration of soil cation exchange capacity.

[38] Several studies corroborate our results for SO_4^{2-} and Cl^- . Average $[\text{SO}_4^{2-}]$ remained three times higher in a Canadian Shield stream for 5 years after fire, and was still above normal 9 years after fire [Bayley et al., 1992]. Sulfate was up to an order of magnitude higher in ephemeral streams for 1 year after fire in mixed-conifer forest in the Lake Tahoe basin [Stephens et al., 2004] (Cl^- was not measured). Prescribed burns in Canadian Shield catchments raised $[\text{SO}_4^{2-}]$ and $[\text{Cl}^-]$ in lakes initially by a factor of three, compared to reference lakes; concentrations were still

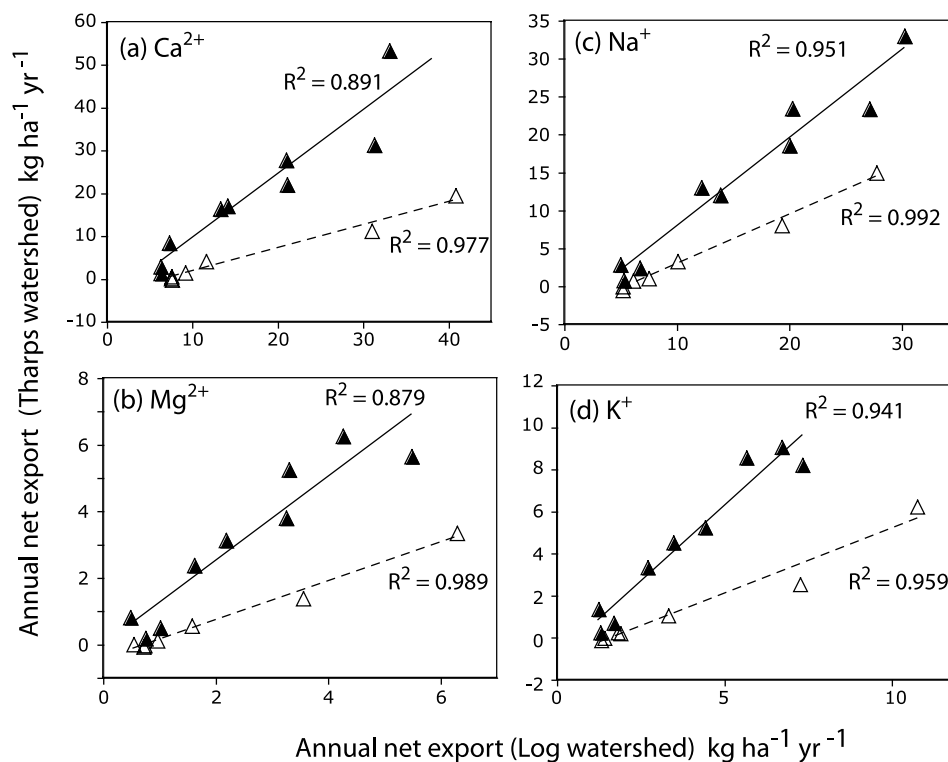


Figure 9. Relationships between annual net export from Tharps watershed and Log watershed for (a) Ca^{2+} , (b) Mg^{2+} , (c) Na^+ , and (d) K^+ , during prefire years (1984–1990, open symbols) and postfire years (1991–1999, solid symbols). Net export <0 indicates net watershed retention. All regression lines shown are significant ($p < 0.05$). For all species, the slopes (but not the intercepts) of the prefire and postfire regression equations were significantly different ($p < 0.05$).

above reference levels after 3 years [Carignan *et al.*, 2000; Lamontagne *et al.*, 2000]. Several investigators report net export of Cl^- from forested watersheds following clear cutting [Dahlgren and Driscoll, 1994; Kauffman *et al.*, 2003; Rosen, 1990] or after wildfire [Bayley *et al.*, 1992]. Chloride is a known plant micronutrient, and releases of Cl^- after forest disturbance could result both from remineralization of Cl^- in organic matter and decreases in plant uptake.

[39] Unexplained export of Cl^- occurred in the control catchment. Either a rough annual balance, or net retention, of Cl^- was observed in Log watershed during dry years (1987–1992, 1994) (Figure 6). In contrast, in wet years, export exceeded deposition of Cl^- by factors as high as three (Figure 6). Over the course of 16 years, Log watershed exported $>13 \text{ kg ha}^{-1}$ more Cl^- than it received from the atmosphere (see net export rate in Table 1). These results indicate depletion of some previously accumulated stockpile of Cl^- within the control catchment, or an unmeasured input. Weathering is an unlikely source of Cl^- in soils developing on granite and granodiorite colluvium [Huntington and Akeson, 1987]. There is evidence that Cl^- from precipitation can be stored in soil during years when runoff is insufficient to fully flush it from soil, and that it is returned to drainage waters quickly after runoff is restored [Kauffman *et al.*, 2003]. Our results indicate that use of Cl^- as a conservative tracer of water fluxes [e.g., see Johnson *et al.*, 1997] may not be warranted in some Sierran forests.

[40] Fire created several avenues for long term SO_4^{2-} export in Tharps watershed. These include oxidation of

organic S in mineral soil [Blank and Zamudio, 1998; Stanko and Fitzgerald, 1990], eventual release of SO_4^{2-} from ash (with some portion cycling through microbial mass, or temporarily held by exchange complexes), decomposition of dead aboveground and belowground tree biomass, and decreased plant uptake. Regardless of the source, it appears that the supply of SO_4^{2-} available for export was diminished in the burned catchment after 9 years (compare 1993 with 1999, years with similar runoff, in Figures 6b and 8b), or that mechanisms for watershed retention of S were recovering (note resumption of net retention of S in 1999, Figure 6).

[41] Interestingly, the cumulative net export of SO_4^{2-} S from Tharps watershed during 9 years following fire (7.9 kg S ha^{-1} , from 1991–1999, Table 2) was nearly equal to the cumulative net retention of atmospheric S in Tharps watershed during the 7 years preceding fire (8.1 kg S ha^{-1}).

4.2. Postfire Export Compared to Prefire Standing Stocks

[42] Different prefire and postfire relationships between solute export from the control and treatment catchments (Figures 8–10) allow us to quantify how much solute export from the treatment catchment resulted from pools or processes established after fire, as opposed to processes that occurred throughout the study. In Table 2, we use solute export from the control catchment (Log watershed) from each postfire year, and the prefire regression equations, to predict solute export during postfire years that would have

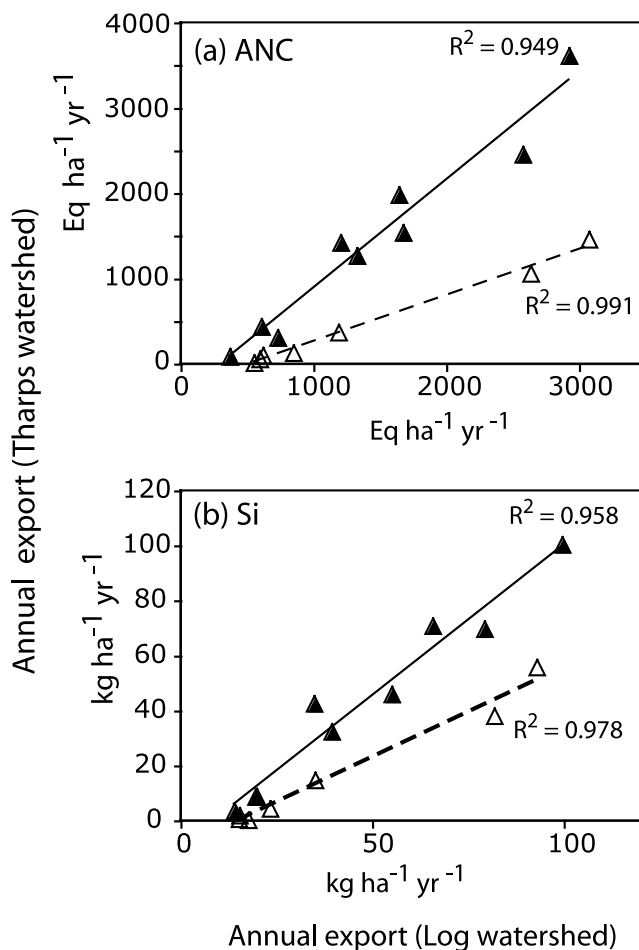


Figure 10. Relationship between annual export from Tharps watershed and Log watershed for (a) acid neutralizing capacity (ANC) and (b) SiO₂ during prefire years (1984–1990, open symbols) and postfire years (1991–1999, solid symbols). Regression lines are significant ($p < 0.05$). For both species, the slopes (but not the intercepts) of the prefire and postfire regression equations were significantly different ($p < 0.05$).

occurred in the treatment catchment (Tharps watershed) regardless of fire. Using this approach, we estimate that fire led to the additional cumulative export, per hectare, of 1.2 kg N, 16 kg S, 25 kg Cl⁻, 130 kg Ca²⁺, 19 kg Mg²⁺, 71 kg Na⁺, 29 kg K⁺, and 192 kg Si, after 9 years (Table 2).

[43] Based on long-term average rates, net accumulation of atmospheric N and S in undisturbed forest becomes equivalent to the fire-related catchment export of these elements after <1 and 20 years, respectively. Volatilization losses of N and DON export, not included in our fire-related losses, would increase replacement times for N. Based on long term net export rates from undisturbed forest, weathering at the study site produces excess Ca²⁺, Mg²⁺, Na⁺, and K⁺ (per hectare) equal to the 9-year fire-related losses of these species after about 8, 8, 5, and 7 years, respectively. Unexplained export of Cl⁻ from undisturbed forest makes it difficult to evaluate replacement times for fire-related losses of this species. However, if atmospheric inputs of Cl⁻ were completely retained after fire, about 20 years would be necessary to replace the fire-related losses of Cl⁻.

[44] Total fuel load before the fire in Tharps watershed (1000-, 100-, 10- and 1-hour fuels) was estimated at 210 Mg ha⁻¹ by *Mutch and Parsons* [1998]. The forest floor (litter and duff) was 35% of total fuel mass. Postfire fuel inventories revealed that the surface litter (O1) and the duff layer (O2) was 97% burnt, producing a loss of 72 Mg ha⁻¹ [Mutch and Parsons, 1998] and leaving a layer of ash 5–30 cm deep on the mineral soil [Chorover *et al.*, 1994]. *Stohlgren* [1988a] measured the mass of aged litter and duff at our study site, and the percent contribution of each of the four dominant tree species to the mass of small debris in the surface litter (Table 3). He also measured the nutrient content of fresh litter from each tree species, and changes after 3.6 years of decomposition (by which time most of the change in the elemental content took place) [Stohlgren, 1988b]. Using Stohlgren's data, we estimate that the aged litter and duff layer at Tharps contained, per hectare, 441–683 kg N, 499–1085 kg Ca, 54–68 kg Mg, and 38–63 kg K before the fire (Table 3). These estimates are reasonable compared to measurements made in other Sierra Nevada forests [Davidson *et al.*, 1992; Johnson *et al.*, 2005].

[45] Using our estimates of elemental mass in the litter and duff layer, and the information in Table 3, we estimate that the cumulative net export of DIN after fire was equal to <1% of the N present in the forest floor (litter and duff) prior to its combustion. We estimate that fire-related losses of Ca, Mg, and K during 9 years of stream export accounted for the following percentages of the base cation mass contained in the burned litter and duff layer (ranges reflect the forest floors of fir- versus giant sequoia-dominated plots):

Ca :	12% to 26%
Mg:	28% to 35%
K :	46% to 76%

Because we did not include the mass of larger fuels in these calculations, these percentages should be smaller. Lacking data on forest floor S, Na, Cl⁻, and Si, we are unable to place observed export for these elements into the same context. Estimates of S content in the forest floor of Jeffrey pine forest in the eastern Sierra Nevada range from 15–19 kg S ha⁻¹ [Johnson *et al.*, 2005; Murphy *et al.*, 2006a]. Interestingly, this range compares well with the cumulative fire-related loss of S from Tharps watershed during the postfire period in our study (16 kg S ha⁻¹).

5. Conclusions

[46] Our results suggest that natural fire-return intervals close to the lower end of historical variability might prevent complete reaccumulation of fire-related losses of S, Cl⁻, Si, and base cations between successive fires. Replacement times for individual species, based on watershed balances in undisturbed forest, range from <1 year (for DIN), to at least 20 years (for Cl⁻ and S). However, these numbers underestimate the time required to rebuild standing stocks after fire. Volatilization losses analogous to those observed in other Sierran forests could boost recovery time for N in Giant Forest as high as 30 years. The persistent increase in water yield we observed in burned forest (and other ecosystem changes) will prolong recovery times for other

Table 3. Estimated Mass of Selected Macronutrients in Aged Litter and Duff in Two Kinds of Forest Plots in Giant Forest^a

	Forest Plot	% Dry Mass of Species in Small Litter Debris, ^b %	Mass of Litter and Duff From Each Species, ^c kg ha ⁻¹	Elemental Content of Fresh Litter, ^d %	Elemental Mass in Fresh Litter, kg ha ⁻¹	% Change in Elemental Mass After 3.6 Year Decay, ^e %	Estimated Mass of Element in Aged Litter and Duff, kg ha ⁻¹
<i>Nitrogen</i>							
Type 1	giant sequoia	48	46512	0.5	233	155	361
	white fir	49	47481	0.7	332	90	299
	sugar pine	3	2907	0.7	20	115	23
							Σ = 683
Type 2	sugar pine	69	50991	0.7	357	80	292
	white fir	22	16258	0.7	114	95	111
	incense cedar	10	7390	0.6	44	105	47
							Σ = 441
<i>Calcium</i>							
Type 1	giant sequoia	48	46512	2.4	1116	50	558
	white fir	49	47481	2.1	997	50	499
	sugar pine	3	2907	1.0	29	95	28
							Σ = 1085
Type 2	sugar pine	69	50991	1.0	510	70	357
	white fir	22	16258	1.5	244	50	122
	incense cedar	10	7390	2.7	200	10	20
							Σ = 499
<i>Magnesium</i>							
Type 1	giant sequoia	48	46512	0.2	93	35	33
	white fir	49	47481	0.2	95	35	23
	sugar pine	3	2907	0.2	6	45	3
							Σ = 68
Type 2	sugar pine	69	50991	0.2	102	40	40
	white fir	22	16258	0.2	33	30	10
	incense cedar	10	7390	0.2	15	20	3
							Σ = 54
<i>Potassium</i>							
Type 1	giant sequoia	48	46512	0.2	93	30	28
	white fir	49	47481	0.4	190	17	32
	sugar pine	3	2907	0.2	6	45	3
							Σ = 63
Type 2	sugar pine	69	50991	0.3	153	18	28
	white fir	22	16258	0.5	81	10	8
	incense cedar	10	7390	0.3	22	10	2
							Σ = 38

^aType 1 forest plots were dominated by giant sequoia, white fir, and sugar pine. Type 2 forest plots were dominated by white fir, sugar pine, and incense cedar.

^bFrom *Stohlgren* [1988a, Table 4].

^cCalculated using a total mass of litter + duff of 96,900 kg ha⁻¹ and 73,900 kg ha⁻¹ for Type 1 and Type 2 forest plots, respectively [from *Stohlgren*, 1988a, Table 7].

^dFrom *Stohlgren* [1988b, Table 3].

^eEstimated from Figure 1 in *Stohlgren* [1988b].

elements. Rebuilding of elemental stocks will depend on how quickly watershed balances return to normal ranges. For example, net retention of S did not resume in the burned catchment until the ninth year after fire. Consequently, recovery time for S stocks in Giant Forest may be closer to 30 years (9 + 20 years). Above-normal export of all other species, except for N, was still taking place 9 years after fire.

[47] Precipitation strongly influenced the magnitude of postfire export. Delayed export of elements from pools established by fire occurred during wet years, even late in our study. A strong El Niño year 8 years after the fire (1998) produced the largest fire-related annual export of several species (Ca²⁺, Mg, Na⁺, Si) observed during the study. If the burn had taken place during a wet year, or had been followed more closely by wet years, higher export of most

species would probably have occurred closer to the fire, and cumulative losses may have been higher.

[48] Considering that the site had been fire-free for over 120 years prior to the experimental burn, postfire changes in Tharps watershed were probably accentuated. Fuel levels prior to the burn were extraordinarily high compared to estimated historical values. Pools of elements available for export would probably have been smaller had less fuel burned. A lower intensity fire likely would have resulted in lower tree mortality, which may have had a smaller, or less persistent, effect on postfire water yield. In our case, however, fire-enhanced loss rates of water and all species, except for DIN, persisted through the end of the study, 9 years after fire. Given that large tracts of Sierra Nevada forest remain unburned since the early 1900s, prolonged changes in watershed balances may be a more common result of prescribed fire than previously expected.

[49] **Acknowledgments.** The watershed program in Sequoia and Kings Canyon National Parks was made possible by the scientific leadership and organizational skills of David Parsons, David Graber, Thomas Stohlgren, and Ray Herrmann. Funding was initially provided by the National Acidic Precipitation Assessment Program in cooperation with the National Park Service. Cooperative efforts with the California Air Resources Board, Electrical Power Research Institute, U.S. Geological Survey, USDA Forest Service, and several universities, added depth to the program. The last 4 years of the watershed program were directed by the U.S. Geological Survey, Biological Resources Division. A portion of the final manuscript preparation was supported by the National Science Foundation (grant DEB 0089389). We thank Anne Pfaff, Patti Haggerty, Amy Workinger, Dan Everson, Lisa Hammett, and Andi Heard for their roles in the program. We are grateful to Al Leydecker, Peter Rowlands, and an anonymous reviewer for thorough comments on the manuscript.

References

- American Public Health Association (APHA) (1981), *Standard Methods for the Examination of Water and Wastewater*, 15th ed., Washington, D. C.
- Bancroft, L., T. Nichols, D. Parsons, D. Graber, B. Evison, and J. Van Wagendonk (1985), Evolution of the natural fire management program at Sequoia and Kings Canyon National Parks, in *Proceedings of the Symposium and Workshop on Wilderness Fire*, edited by J. E. Lotan, B. M. Kilgore, W. C. Fischer, and R. W. Mutch, *Gen. Tech. Rep. INT-182*, pp. 174–180, U.S. Dep. of Agric. For. Serv., Intermountain For. and Range Exp. Stn., Ogden, Utah.
- Bayley, S. E., D. W. Schindler, B. R. Parker, M. P. Stainton, and K. G. Beaty (1992), Effects of forest fire and drought on acidity of a base-poor boreal forest stream: Similarities between climatic warming and acidic precipitation, *Biogeochemistry*, 17, 191–204.
- Bech, L. A., S. L. Stephens, and V. H. Resh (2005), Effects of prescribed fire on a Sierra Nevada (California, USA) stream and its riparian zone, *For. Ecol. Manage.*, 218, 37–59.
- Blank, R. R., and D. C. Zamudio (1998), The influences of wildfire on aqueous-extractable soil solutes in forested and wet meadow ecosystems along the eastern front of the Sierra-Nevada Range, California, *Int. J. Wildl. Fire*, 8, 79–85.
- Blew, R. D., D. Iredale, and D. Parkinson (1993), Throughfall nitrogen in a white spruce forest in southwest Alberta, Canada, *Can. J. For. Res.*, 23, 2389–2394.
- Bytnerowicz, A., M. Tausz, R. Alonso, D. Jones, R. Johnson, and N. Grulke (2002), Summer-time distribution of air pollutants in Sequoia National Park, California, *Environ. Pollut.*, 118, 187–203.
- Caldwell, T. G., D. W. Johnson, W. W. Miller, and R. G. Qualls (2002), Forest floor carbon and nitrogen losses due to prescription fire, *Soil Sci. Am.*, 66, 262–267.
- Caprio, A. C., and D. M. Graber (2000), Returning fire to the mountains: Can we successfully restore the ecological role of pre-European fire regimes to the Sierra Nevada, in *Wilderness Science in a Time of Change Conference*, vol. 5, edited by D. N. Cole, S. F. McCool, and J. O'Loughlin, *RMRS-P-15*, pp. 233–241, U.S. Dep. of Agric. For. Serv., Rocky Mtn. Res. Stn., Missoula, Mont.
- Carignan, R., P. D'Arcy, and S. Lamontagne (2000), Comparative impacts of fire and forest harvesting on water quality in Boreal Shield lakes, *Can. J. Fish. Aquat. Sci.*, 57(suppl. 2), 105–117.
- Cerda, A. (1998), Changes in overland flow and infiltration after a range-land fire in a Mediterranean scrubland, *Hydrol. Processes*, 12, 1031–1042.
- Chorover, J., P. M. Vitousek, D. A. Everson, A. M. Esperanza, and D. Turner (1994), Solution chemistry profiles of mixed-conifer forests before and after fire, *Biogeochemistry*, 26, 115–144.
- Coats, R. N., and C. R. Goldman (2001), Patterns of nitrogen transport in streams of the Lake Tahoe basin, California-Nevada, *Water Resour. Res.*, 37, 407–415.
- Collett, J. L., Jr., B. C. Daube Jr., and M. R. Hoffmann (1990), The chemical composition of intercepted cloudwater in the Sierra Nevada, *Atmos. Environ.*, 24A, 959–972.
- Dahlgren, R. A., and C. T. Driscoll (1994), The effects of whole-tree clear-cutting on soil processes at the Hubbard Brook experimental forest, New Hampshire, USA, *Plant Soil*, 158, 239–262.
- Davidson, E. A., S. C. Hart, and M. K. Firestone (1992), Internal cycling of nitrate in soils of a mature coniferous forest, *Ecology*, 73, 1148–1156.
- Derry, L. A., A. C. Kurtz, K. Ziegler, and O. A. Chadwick (2005), Biological control of terrestrial silica cycling and export fluxes to watersheds, *Nature*, 433, 728–731.
- Ewing, R. (1996), Postfire suspended sediment from Yellowstone National Park, Wyoming, *Water Res. Bull.*, 32, 605–627.
- Fahey, T. J., J. B. Yavitt, and G. Joyce (1988), Precipitation and throughfall chemistry in *Pinus contorta* ssp. *latifolia* ecosystems, southeastern Wyoming, *Can. J. For. Res.*, 18, 337–345.
- Fenn, M. E., M. A. Poth, S. L. Schilling, and D. B. Grainger (2000), Throughfall and fog deposition of nitrogen and sulfur at an N-limited and N-saturated site in the San Bernardino Mountains, southern California, *Can. J. For. Res.*, 30, 1476–1488.
- Fenn, M. E., et al. (2003), Nitrogen emissions, deposition, and monitoring in the western United States, *Bioscience*, 53, 391–403.
- Friedland, A. J., and E. K. Miller (1999), Major-element cycling in a high-elevation Adirondack forest: patterns and changes, 1986–1996, *Ecol. Appl.*, 9, 958–967.
- Fuller, R. D., C. T. Driscoll, G. Lawrence, and S. C. Nodvin (1987), Processes regulating sulphate flux after whole-tree harvesting, *Nature*, 325, 707–710.
- Gerla, P. J., and J. M. Galloway (1997), Water quality of two streams near Yellowstone Park, Wyoming, following the 1988 Clover-Mist wildfire, *Environ. Geol.*, 36, 127–136.
- Grabow, G. L., J. Spooner, L. A. Lombardo, D. E. Line, and K. L. Tweedy (1998), Has water quality improved?: Use of a spreadsheet for statistical analysis of paired watershed, upstream/ downstream and before/after monitoring designs, paper presented at Sixth National Nonpoint-Source Monitoring Workshop, U.S. Environ. Prot. Agency, Cedar Rapids, Iowa, 21–24 Sept.
- Gran, G. (1952), Determination of the equivalent point in potentiometric titrations: Part 2, *Analyst*, 77, 661–671.
- Halpin, P. N. (1995), A cross-scale analysis of environmental gradients and forest pattern in the giant sequoia–mixed conifer forest of the Sierra Nevada, Ph.D. dissertation, Duke Univ., Durham, N. C.
- Hanson, P. J., and S. E. Lindberg (1991), Dry deposition of reactive nitrogen compounds: a review of leaf, canopy and non-foliar measurements, *Atmos. Environ.*, 25A, 1615–1634.
- Helvey, J. D. (1980), Effects of a north central Washington wildfire on runoff and sediment production, *Water Res. Bull.*, 16, 627–634.
- Hicks, B. B., R. P. Hosker, T. P. Meyers, and J. D. Womack (1991), Dry deposition inferential measurement techniques. 1. Design and tests of a prototype meteorological and chemical system for determining dry deposition, *Atmos. Environ.*, 25, 2345–2359.
- Huffman, E. L., L. H. MacDonald, and J. D. Stednick (2001), Strength and persistence of fire-induced soil hydrophobicity under ponderosa and lodgepole pine, Colorado Front Range, *Hydrol. Processes*, 15, 2877–2892.
- Huntington, G. L., and M. A. Akeson (1987), Pedologic investigations in support of acid rain studies: Soil resource inventory of Sequoia National Park, Central Part, California, *Natl. Park Serv. Rep.*, CA 8005-2-0002.
- Johnson, D. W., R. B. Susfalk, and R. A. Dahlgren (1997), Nutrient fluxes in forests of the eastern Sierra Nevada mountains, United States of America, *Global Biogeochem. Cycles*, 11, 673–681.
- Johnson, D. W., J. F. Murphy, R. B. Susfalk, T. G. Caldwell, W. W. Miller, R. F. Walker, and R. F. Powers (2005), The effects of wildfire, salvage logging, and postfire N-fixation on the nutrient budgets of a Sierran forest, *For. Ecol. Manage.*, 220, 155–165.
- Kauffman, S. J., D. L. Royer, S. Chang, and R. A. Berner (2003), Export of chloride after clear-cutting in the Hubbard Brook sandbox experiment, *Biogeochemistry*, 63, 23–33.
- Kaye, J. P., and S. C. Hart (1998), Ecological restoration alters nitrogen transformations in a ponderosa pine-bunchgrass ecosystem, *Ecol. Appl.*, 8, 1052–1060.
- Keeley, J. E., and N. L. Stephenson (2000), Restoring natural fire regimes in the Sierra Nevada in an era of global change, in *Wilderness Science in a Time of Change Conference*, vol. 5, edited by D. N. Cole, S. F. McCool, and J. O'Loughlin, *RMPS-P-15*, pp. 255–265, U.S. Dep. of Agric. For. Serv., Rocky Mtn. Res. Stn., Missoula, Mont.
- Keifer, M. (1998), Fuel load and tree density changes following prescribed fire in the giant sequoia–mixed conifer forest: the first 14 years of fire effects monitoring, in *Proceedings of 20th Tall Timbers Fire Ecology Conference*, edited by T. L. Pruden and L. A. Brennan, pp. 306–309, Tall Timbers Res. Stn., Tallahassee, Fla.
- Knapp, E. E., J. E. Keeley, E. A. Ballenger, and T. J. Brennan (2005), Fuel reduction and coarse woody debris dynamics with early season and late season prescribed fires in a Sierra Nevada mixed conifer forest, *Forest Ecol. Manage.*, 208, 383–397.
- Knoepp, J. D., and W. T. Swank (1995), Comparison of available soil nitrogen assays in control and burned forest sites, *Soil Sci. Soc. Am. J.*, 59, 1750–1754.
- Lamontagne, S., R. Carignan, P. D'Arcy, Y. T. Prairie, and D. Paré (2000), Element export in runoff from eastern Canadian Boreal Shield drainage basins following forest harvesting and wildfires, *Can. J. Fish. Aquat. Sci.*, 57, 118–128.

- Lavabre, J., D. S. Torres, and F. Cernesson (1993), Changes in hydrological response of a small Mediterranean basin a year after a wildfire, *J. Hydrol.*, **142**, 273–299.
- Lindberg, S. E., G. M. Lovett, D. D. Richter, and D. W. Johnson (1986), Atmospheric deposition and canopy interactions of major ions in a forest, *Science*, **231**, 141–145.
- Mabuhay, J. A., Y. Isagi, and N. Nakagoshi (2006), Wildfire effects on microbial biomass and diversity in pine forests at three topographic positions, *Ecol. Res.*, **21**, 54–63.
- MacDonald, L. H., and E. L. Huffman (2004), Postfire soil water repellency: persistence and soil moisture thresholds, *Soil Sci. Am. J.*, **68**, 1729–1734.
- MacKenzie, M. D., T. H. DeLuca, and A. Sala (2006), Fire exclusion and nitrogen mineralization in low elevation forests of western Montana, *Soil Biol. Biochem.*, **38**, 952–961.
- Markewitz, D., and D. D. Richter (1998), The bio in aluminum and silicon geochemistry, *Biogeochemistry*, **42**, 235–252.
- Martin, D. A., and J. A. Moody (2001), Comparison of soil infiltration rates in burned and unburned mountainous watershed, *Hydrol. Processes*, **15**, 2893–2903.
- McNabb, D. H., F. Gaweda, and H. A. Froehlich (1989), Infiltration, water repellency, and soil moisture content after broadcast burning a forest site in southwest Oregon, *J. Soil Water Conserv.*, **44**, 87–90.
- Melack, J. M., and J. L. Stoddard (1991), Sierra Nevada, California, in *Acidic Deposition and Aquatic Ecosystems, Regional Case Studies*, edited by D. R. Charles, chap. 15, pp. 503–530, Springer, New York.
- Meyers, T. P., B. B. Hicks, R. P. Hosker, J. D. Womack, and L. C. Satterfield (1991), Dry deposition inferential measurement techniques. 2. Seasonal and annual deposition rates of sulfur and nitrate, *Atmos. Environ.*, **25**, 2361–2370.
- Meyers, T. P., P. Finkelstein, J. Clarke, T. G. Ellestad, and P. F. Sims (1998), A multilayer model for inferring dry deposition using standard meteorological measurements, *J. Geophys. Res.*, **103**, 22,645–22,661.
- Moore, C. M., and J. E. Keeley (2000), Long-term hydrologic response of a forested catchment to prescribed fire, in *Water Resources in Extreme Environments, Proceedings of American Water Resources Association*, edited by D. Kan, Am. Water Resour. Assoc., Middleburg, Va.
- Murphy, J. D., D. W. Johnson, W. W. Miller, R. F. Walker, and R. R. Blank (2006a), Prescribed fire effects on forest floor and soil nutrients in a Sierra Nevada forest, *Soil Sci.*, **171**, 181–199.
- Murphy, J. D., D. W. Johnson, W. W. Miller, R. F. Walker, E. F. Carroll, and R. R. Blank (2006b), Wildfire effects on soil nutrients and leaching in a Tahoe Basin watershed, *J. Environ. Qual.*, **35**, 479–489.
- Mutch, L. S., and D. J. Parsons (1998), Mixed conifer forest mortality and establishment before and after prescribed fire in Sequoia National Park, California, *For. Sci.*, **44**, 341–355.
- Norby, R. J., Y. Weerasuriya, and P. J. Hanson (1989), Induction of nitrate reductase activity in red spruce needles by NO₂ and HNO₃ vapor, *Can. J. For. Res.*, **19**, 889–896.
- Nussbaum, S., P. Von Ballmoos, H. Gfeller, U. P. Schlunegger, J. Fuhrer, D. Rhodes, and C. Brunold (1993), Incorporation of atmospheric HNO₃-nitrogen into free amino acids by Norway spruce *Picea abies* (L.) Karst., *Oecologia*, **94**, 408–414.
- Oakley, B. B., M. P. North, and J. F. Franklin (2003), The effects of fire on soil nitrogen associated with patches of the actinorhizal shrub *Ceanothus cordulatus*, *Plant Soil*, **254**, 35–46.
- Prosser, I. P., and L. Williams (1998), The effect of wildfire on runoff and erosion in native *Eucalyptus* forest, *Hydrol. Processes*, **12**, 251–265.
- Raison, R. J., P. K. Khann, and P. V. Woods (1985), Mechanisms of element transfer to the atmosphere during vegetation fires, *Can. J. For. Res.*, **15**, 132–140.
- Robichaud, P. R. (2000), Fire effects on infiltration rates after prescribed fire in northern Rocky Mountain forests, USA, *J. Hydrol.*, **231/232**, 220–229.
- Robichaud, P. R., and T. A. Waldrop (1994), A comparison of surface runoff and sediment yields from low and high-severity site preparation burns, *Water Res. Bull.*, **30**, 27–34.
- Rosen, K. (1990), Measuring nutrient input to terrestrial ecosystems, in *Nutrient Cycling in Terrestrial Ecosystems*, edited by A. F. Harrison and P. Ineson, pp. 1–10, Elsevier, London.
- Schoch, P., and D. Binkley (1986), Prescribed burning increased nitrogen availability in a mature loblolly pine stand, *For. Ecol. Manage.*, **14**, 13–22.
- Sickman, J. O., A. Leydecker, and J. M. Melack (2001), Nitrogen mass balances and abiotic controls on N retention and yield in high-elevation catchments of the Sierra Nevada, California, United States, *Water Resour. Res.*, **37**, 1445–1461.
- Soil Survey Staff (2006), *Keys to Soil Taxonomy*, 10th ed., 331 pp., U.S. Dep. of Agric., Nat. Resour. Conserv. Serv., Washington, D. C.
- Sommer, M., D. Kaczorek, Y. Kuzyakov, and J. Breuer (2006), Silicon pools and fluxes in soils and landscapes—A review, *J. Plant Nutr. Soil Sci.*, **169**, 310–329, doi:10.1002/jpln.200521981.
- Stanko, K. M., and J. W. Fitzgerald (1990), Sulfur transformations in forest soils collected along an elevational gradient, *Soil. Biol. Biochem.*, **22**, 213–216.
- Stephens, S. L., T. Meixner, M. Poth, B. McGurk, and D. Payne (2004), Prescribed fire, soils, and stream water chemistry in a watershed in the Lake Tahoe basin, California, *Int. J. Wildl. Fire*, **13**, 1–9.
- Stephenson, N. L. (1996), Ecology and management of giant sequoia groves, in *Sierra Nevada Ecosystem Project: Final Report to Congress*, vol. 2, *Assessments and Scientific Basis for Management Options*, Wildl. Res. Cent. Rep. 37, Cent. for Water and Wildl. Resour., Univ. of Calif., Davis.
- Stephenson, N. L. (1999), Reference conditions for giant sequoia forest restoration: structure, process, and precision, *Ecol. Appl.*, **9**, 1253–1265.
- Stephenson, N. L., D. J. Parson, and T. W. Swetnam (1991), Restoring natural fire to the sequoia–mixed conifer forest: Should intense fire play a role?, in *Proceedings of 17th Tall Timbers Fire Ecology Conference*, edited by S. M. Hermann, pp. 321–337, Tall Timbers Res. Stn., Tallahassee, Fla.
- Stohlgren, T. J. (1988a), Litter dynamics in two Sierran mixed conifer forests. I. Litterfall and decomposition rates, *Can. J. For. Res.*, **18**, 1127–1135.
- Stohlgren, T. J. (1988b), Litter dynamics in two Sierran mixed conifer forests. II. Nutrient release in decomposing leaf litter, *Can. J. For. Res.*, **18**, 1136–1144.
- Stohlgren, T. J., J. M. Melack, A. M. Esperanza, and D. J. Parsons (1991), Atmospheric deposition and solute export in giant sequoia–mixed conifer watersheds in the Sierra Nevada, California, *Biogeochemistry*, **12**, 207–230.
- Stottliemyer, R. (1987), Natural and anthropic factors as determinants of long-term stream water chemistry, in *Management of Subalpine Forests: Building on 50 Years of Research*, edited by C. A. Troendle, M. R. Kaufman, R. H. Hamre, and R. P. Winokur, *Gen. Tech. Rep. RM-149*, pp. 86–94, U.S. Dep. of Agric. For. Serv. Rocky Mountn. For. and Range Exp. Stn., Ft. Collins, Colo.
- Stottliemyer, R., and C. A. Troendle (1987), Trends in stream water chemistry and input-output balances, Fraser Experimental Forest, Colorado, *Res. Pap. RM-275*, U.S. Dep. of Agric. For. Serv., Rocky Mountn. For. and Range Exp. Stn., Fort Collins, Colo.
- Stottliemyer, R., and C. A. Troendle (1999), Effect of subalpine canopy removal on snowpack, soil solution, and nutrient export, Fraser Experimental Forest, CO, *Hydrol. Processes*, **13**, 2287–2299.
- Stottliemyer, R., and C. A. Troendle (2001), Effect of canopy removal on snowpack quantity and quality, Fraser experimental forest, Colorado, *J. Hydrol.*, **245**, 165–176.
- Strickland, J. D. H., and T. R. Parsons (1972), *A Practical Handbook for Seawater Analysis*, 2nd ed., *Bull. 167*, Fish. Res. Bd. of Can., Ottawa.
- Swetnam, T. W., C. H. Baisan, A. C. Caprio, R. Touchan, and P. M. Brown (1992), Tree-ring reconstruction of giant sequoia fire regimes, final report on cooperative agreement DOI 80181-0002, Natl. Park Serv., Sequoia and Kings Canyon Natl. Parks, Calif.
- Tumbusch, M. L. (2003), Evaluation of OTT PLUVIO Precipitation Gage versus Belfort Universal Precipitation Gage 5–780 for the National Atmospheric Deposition Program, *U.S. Geol. Surv. Water Resour. Invest. Rep.*, **03–4167 A**.
- Valderrama, J. C. (1981), The simultaneous analysis of total nitrogen and total phosphorus in natural waters, *Mar. Chem.*, **10**, 109–122.
- Van Mantgem, P. J., N. L. Stephenson, M. B. Keifer, and J. E. Keeley (2004), Effects of an introduced pathogen and fire exclusion on demography of sugar pine, *Ecol. Appl.*, **14**, 1590–1602.
- Vitousek, P. M., J. R. Gosz, C. C. Grier, J. M. Melillo, and W. A. Reiners (1982), A comparative analysis of potential nitrification and nitrate mobility in forest ecosystems, *Ecol. Monogr.*, **52**, 155–177.
- Wan, S., D. Hui, and Y. Luo (2001), Fire effects on nitrogen pools and dynamics in terrestrial ecosystems: a meta-analysis, *Ecol. Appl.*, **11**, 1349–1365.
- Whicker, J. J., J. E. Pinder, and D. D. Breshears (2006), Increased wind erosion from forest wildfire: Implications for contaminant-related risks, *J. Environ. Qual.*, **35**, 468–478.
- White, C. S. (1986), Effects of prescribed fire on rates of decomposition and nitrogen mineralization in a ponderosa pine ecosystem, *Biol. Fertil. Soils*, **2**, 87–95.
- Williams, M. R., and J. M. Melack (1997a), Atmospheric deposition, mass balances, and processes regulating stream water solute concentrations in mixed-conifer catchments of the Sierra Nevada, California, *Biogeochemistry*, **37**, 111–144.
- Williams, M. R., and J. M. Melack (1997b), Effects of prescribed burning and drought on the solute chemistry of mixed-conifer forest streams of the Sierra Nevada, California, *Biogeochemistry*, **39**, 225–253.
- Williams, M. W., A. D. Brown, and J. M. Melack (1993), Geochemical and hydrologic controls on the composition of surface water in a high-elevation basin, Sierra Nevada, California, *Limnol. Oceanogr.*, **38**, 775–797.

- Wright, R. J., and S. C. Hart (1997), Nitrogen and phosphorus status in a southwestern ponderosa pine forest after 20 years of interval burning, *Ecoscience*, 4, 526–533.
- Yeager, C. M., D. E. Northup, C. C. Grow, S. M. Barns, and C. R. Kuske (2005), Changes in nitrogen-fixing and ammonia-oxidizing bacterial communities in soil of a mixed conifer forest after wildfire, *Appl. Environ. Microbiol.*, 71, 2713–2722.
-
- D. L. Engle, Marine Science Institute, University of California, Santa Barbara, CA 93106, USA. (drdianaengle@yahoo.com)
- A. M. Esperanza, Division of Natural Resources, Sequoia and Kings Canyon National Parks, Three Rivers, CA 93271, USA.
- J. E. Keeley, U.S. Geological Survey, Western Ecological Research Center, Sequoia and Kings Canyon National Parks, Three Rivers, CA 93271, USA.
- J. M. Melack, Department of Ecology, Evolution, and Marine Biology and Donald Bren School of Environmental Science and Management, University of California, Santa Barbara, CA 93106, USA.
- C. M. Moore, National Park Service, Inventory and Monitoring Program, Southwest Alaska Network, Katmai National Park and Preserve, King Salmon, AK 99613, USA.
- J. O. Sickman, Department of Environmental Sciences, University of California, Riverside, CA 92521, USA.